

The Interaction of Predators and
 "Eyespot Butterflies" Feeding on Rotting Fruits and
 Soupy Fungi in Tropical Forests:
 Variations on a Theme Developed by the
 Muysmondts and Arthur M. Shapiro

By DR. ALLEN M. YOUNG *

In recent volumes of *The Entomologist's Record*, two interesting reports by A. Muysmondts Sr. and Jr. (*The Entomologist's Record*, **88**: 283-285) and Dr. A. M. Shapiro (*The Entomologist's Record*, **89**: 293-295) have emphasized that few, if any, large butterflies in flight, in both temperate and tropical regions are successfully attacked and eaten by birds. However, the Muysmondts and Dr. Shapiro point out that resting butterflies are probably attacked frequently by vertebrate predators. The Muysmondts point out that they sometimes encounter in nature butterflies with very symmetrical pieces missing from both hindwings, indicating an attempted attack ("near miss"). In some previous field studies of adult populations in some species of *Morpho* (Morphidae) in Costa Rica it was possible to observe the frequency of butterflies bearing symmetrical wing damage over many months (Young 1973, *Studies in the Neotropical Fauna*, **8**: 17-50; 1975, *Revista de Biologia Tropical*, **23**: 101-123; Young and Thomason, 1974, *Studies in the Neotropical Fauna*, **9**: 1-34) although this aspect of *Morpho* biology was not discussed to any great degree in those reports. The data from those field studies were re-examined in light of the comments of the Muysmondts and Dr. Shapiro. Furthermore, I add to the discussion to follow, observations on other groups of tropical butterflies that feed on rotting fruits and decaying, soupy fungal growths on the floors of forests. In the lowland and mid-elevation tropical rain forests of Central and South America, a substantial portion of the day-flying and crepuscular Rhopalocera feed on sweet-smelling, highly odoriferous rotting fruits and rotting fungal growths on fresh sap flows that have turned "soupy" as a result of microbial activity. The precise nutritive attributes of such resources for adult butterflies has not been determined, but in the American tropics, three major families of generally medium-to-large butterflies, the Morphidae, Satyridae, and Brassolidae, exploit them as the major if not sole source of food. I term these groups the "eyespot butterflies". In light of a recent discussion on the possible adaptive significance of distinctive eyespot markings on the undersides of the wings of Satyridae, Brassolidae, and Morphidae (Young, 1979, *Journal of the New York Entomological Society*, **87**: 66-77) and the fact that some species of *Morpho* butterflies are attacked by certain birds while in flight (Young, 1972, *Oecologia*, **7**: 209-222), there is a need to ascertain estimates of vertebrate predation on butterflies in nature. The purpose of this note is to

* Invertebrate Zoology Section, Milwaukee Public Museum, Milwaukee, Wisconsin 53233 U.S.A.

call attention to additional qualitative and quantitative data on this phenomenon.

In large day-flying tropical butterflies such as *Morpho*, it is possible to estimate the intensity of predator attacks on flying and resting butterflies by scoring wild-caught individuals for "symmetrical" and "asymmetrical" wing damage. Butterflies with symmetrical wing damage have corresponding pieces missing (of same size and shape) from each of two fore- or hindwings, indicating an unsuccessful predator attack while resting or feeding (with wings closed). Similarly, most instances of unsuccessful pursuit of flying butterflies would be indicated by a beak-type fragment of one wing missing, or an asymmetrical form of wing damage. A distinguishing feature of *Morpho* (and Morphidae) from the Satyridae and Brassolidae, three groups sharing a close but unclear phylogenetic relationship (Ehrlich and Raven, 1965, *Evolution*, **18**: 586-608; Miller, 1968, *Memo. Amer. Ent. Soc.* No. 24. Young and Muysshondt, 1972, *Revista de Biologia Tropical*, **20**: 231-263; Young and Muysshondt, 1975, *Studies in the Neotropical Fauna*, **10**: 19-56), is that most species possess wings with very contrasting upper and lower sides: the upper sides have various hues of blue resulting from scales reflecting certain wavelengths of light (Lippert and Gentil, 1959, *Z. Morph. Okol. Tiere*, **48**: 115-122) while the under sides are various shades of brown marked with eyespots of varying size and conspicuousness. Most satyrids and brassolids are coloured similarly on both wing surfaces, although eyespot markings are largely confined to the under sides. As developed below, such differences between the Morphidae on one hand the Satyridae and Brassolidae on the other, have considerable biological significance.

A striking feature of Central and South American tropical rain forests in the vertical stratification of plant life and distribution of sun light at different levels (Richard, 1964, *The Tropical Rain Forest*, Cambridge University Press, London). Butterflies thriving at different levels in this environmental gradient may be subject to differing selection pressures resulting from the activity of vertebrate predators. Counter-selection in predators occupying different levels is also operative. For some groups of butterflies occupying several levels of the forest, because of differing forms of selection pressure from insectivorous vertebrate predators, species that spend most of their life time in a certain level may evolve morphological and behavioural traits different from congeners occupying other levels. For example, adult *Morpho* butterflies can be classified into three groups based on certain behavioural and morphological features: (1) "low fliers-primarily ground feeders-wings with large eyespots"; (2) "intermediate to high fliers-partial ground feeders-wings with small eyespots"; (3) "high fliers-occasional ground feeders-wings with small eyespots". These distinctions apply primarily to extant tropical regions where considerable primary forest is still present, as such relatively undisturbed areas where probably the original

environments ("sphere" of selection pressures) of *Morpho*. Furthermore, these classes are the result of my observations of *Morpho* over the past eleven years, and reports in the literature (e.g., Seitz, 1924, *Macrolepidoptera of the World*, Vol. 5, A. Kernan, Stuttgart), and they do not necessarily reflect any phylogenetic pattern of *Morpho* evolution. Clearly, in terms of the daily flight activities of *Morpho*, these classes are not mutually exclusive, but rather serve as an attempt to characterize the major habitats of different species. "Low fliers" occupy primarily the lower understory and generally fly within two meters of the ground; "Intermediate to high flies" generally occupy transitional understories and fly within 2-6 meters; "High fliers" are primarily canopy-dwellers. For each of these classes the degree of vertebrate predator attack, both for flying and resting (and feeding) individuals, may vary considerably.

In order to examine the possible relationship between frequency of predator attacks in a general way for *Morpho* butterflies in these three classes, I surveyed a series of museum specimens, all wild-caught, and scored each one for symmetrical and asymmetrical wing damage. The data were recorded for each species and over 700 specimens, representing 23 species. Owing to the questionable status of some species, and the possible existence of "super species" complexes, the resulting data are lumped for four species groups ("achilles", "anaxibia", "hecuba", and "catenarius"). The "achilles group" contains the species *achilles* Linnaeus, *achillaena* Fruhst., *peleides* Kollar, *granadensis* Butler, *vitrea* Butler, *patroculus* Hoff., and *deidaema* Hubner. All of these species are strikingly similar in overall appearance, having dull bluish upper wing surfaces with broad black or brown margins, and undersides with very large colourful conspicuous eyespots. The "anaxibia group" consist of species *anaxibia* Esper, *amathonte* Drury, *cypris* Westw., *rhetenor* Staudinger, *menalaus* Butler, *sulkowskyi* Kollar, and *aega* Hubner. All of these species, especially the males, possess brilliant or dazzling blue upper wing surfaces with greatly reduced or no borders, and light brown undersides with small eyespots. The "hecuba group" consists of species *hecuba* Linnaeus, *theseus* Cr., *perseus* Cr., and *hercules* Dalm. All of these species have dull greenish-white upper wing surfaces with large, diffuse brown borders and some have almost entirely brown and orange wings; the undersides are reddish brown with small eyespots. The species of the "catenarius group" are *catenarius* Fruhst., *polyphemus* Dbl. & Hew., *portis* Hubner, *godarti* Guer., and *laertes* Druce. These species possess white, translucent wings (both upper and under sides) with small eyespots. The specimens examined, all in the collections of the Milwaukee Public Museum, came from specific localities in Brazil, Bolivia, British Guyana, French Guyana, Costa Rica, Colombia, Ecuador, Argentina, Peru, Mexico, and El Salvador. More than 80% of the specimens males, which is not unexpected for *Morpho* since females far

more secretive in habits and therefore more difficult to capture in the wild (e.g., Young, 1973, *Studies in the Neotropical Fauna*, 8: 17-50).

Of a total of 388 specimens in the "achilles group" examined, 98 individuals or about 25%, has symmetrical wing damage, and about 4% had asymmetrical damage. For the 163 specimens of the "anaxibia group" examined, only 6 or about 3% had symmetrical damage and 1% had asymmetrical damage to the wings. For 71 specimens of the "hecuba group" examined, none had symmetrical damage and only 3 individuals or about 4% had asymmetrical wing damage. For 92 specimens of the "catenarius group", none had symmetrical wing damage and only 3 or about 3% had asymmetrical damage. Although the sample size for the "achilles group" is considerably larger than the others, there is a disproportionately greater percentage of symmetrical wing damage in this group.

The "achilles group" also falls under the first behavioural-morphological class, namely "low fliers-primarily group feeders-wings with large eyespots". Thus species of *Morpho* in the "achilles group" spend most of their time on and near the ground and feed there. The other species groups are less frequently encountered in these places. The "anaxibia group" falls into the "Intermediate to high fliers-partial group feeders-wings with small eyespots" class while both the "hecuba" and "catenarius" groups fall under the "High fliers-occasional ground feeders-wings with small eyespots" class. Thus species of *Morpho* possessing only small eyespot markings and which are generally high fliers and do not feed primarily on or near the ground, are experiencing the least frequency of unsuccessful attacks by vertebrate predators while resting or feeding. Presumably therefore it is these species which are attacked the least in the wild. The data also indicate that all species of *Morpho* are seldom attacked by birds while flying since the frequency of asymmetrical wing damage is less than 5% in all cases.

In field samples of *Morpho peleides* Kollar studied in Costa Rica over several years (1970-75), in a total of close to 400 individuals captured and released, about 40% had symmetrical wing damages confined to the hindwings (*pers. obs.*). In forest understory habitats where *Morpho* and other butterflies feed on rotting fallen fruits and soupy fungal growths, the *Cnemidophorus* (Teiidae) lizards are active foragers on large-bodied insects (*pers. obs.*). When a captured lizard is induced to bite into the closed hindwings of *Morpho peleides*, the symmetrical wing damage resulting from this artificial attack matches the damage patterns in wild caught butterflies. Wild-caught individuals of *Morpho amathonte* Drury and *Morpho theseus* Cramer in Costa Rica very seldom show these patterns of wing damage. Various types of insectivorous lizards such as *Cnemidophorus* and *Ameiva* are probably the major predators of *Morpho* butterflies on the floor of Costa Rican tropical forests and this may also be the case elsewhere.

Of all the six species of *Morpho* that occur in Costa Rica, by far the most commonly encountered species at experimental fruit baits on forest floors are *Morpho peleides* and where locally abundant, *Morpho granadensis*. Elsewhere (Young, 1979, *Journal of the New York Entomological Society*, 87: 66-77) it was argued that conspicuous eyespot markings on the undersides of wings in the Morphidae, Brassolidae, and Satyridae evolved primarily as an adaptation to lower the chance of successful attack by a visually-hunting vertebrate predator, especially when the intake of fermenting and intoxicating juices may reduce the effectiveness of sensory-motor responses of the butterflies for escape. As for attacks on large flying butterflies, the wing movements in association with reflective colouration play major roles in evasive behaviour of *Morpho* to avian predators (Young, 1972, *Oecologia*, 7: 209-222) although the well known Central American ornithologist Dr. Alexander F. Skutch has observed Rufous-tailed Jacamars (*Galbula ruficauda*) successfully feeding on flying butterflies (*pers. comm.*). In Dr. Skutch's experiences, "jacamars capture more butterflies than any other Central American birds" (*pers. comm.*), perhaps suggesting that most Central American birds do not capture butterflies. Therefore, the greatest predator-type selection pressure is operating on resting or feeding butterflies in agreement with the Muysmondts observations of few if any butterflies being taken in flight. Such selection pressure is greatest for *Morpho* that spend most of their time near or on the ground, and it is probably relaxed for those species occupying the upper regions of the forest.

If the conspicuous colouration of the upperwing surfaces in many species of *Morpho* evolved for both courtship and evasive behaviour against avian predators (Young, 1972, *Oecologia*, 7: 209-222), it may be deleterious to these butterflies when resting or feeding. A sudden flash of blue produced by a sun fleck hitting a group of feeding morphos (Young, 1975, *Revista de Biología Tropical*, 23: 101-123) may attract an active foraging insectivorous vertebrate such as a lizard, and result in an attack. Thus brilliant blue colouration in species of *Morpho* that live near the ground is not adaptive in terms of escape from predators while butterflies are resting or feeding. At rotting banana baits or natural accumulations of sweet-smelling fallen fruits, many other insects accumulate and when *Morpho* is disturbed by these, there results considerable flashing of wings without actual flight. Such situations may increase the probability that feeding butterflies will be detected by predators. Species of *Morpho* feeding higher up in the forest may be less exposed to such factors. Larger eyespot markings in *Morpho* and other butterflies feeding near or on the forest floor may function to either discourage attacks by predators, or provide camouflage colouration for passive escape (Stradling, 1976, *Ecol. Entomol.*, 1: 135-138; Young, 1979, *Journal of the New York Entomol. Soc.*, 87: 66-77). Although the actual levels of successful attacks on feeding or

resting butterflies are not determined, wing caches of *Morpho peleides* in lowland tropical rain forest indicate the vertebrate predation levels can sometimes be high (Young, 1972, *Oecologia*, **7**: 209-222).

The lesson to be learned from *Morpho* in Central and South American rain forests is that species of the large "achilles group" experience the greatest risk of being attacked by vertebrate predators while resting and feeding on the forest floor. These data generally support the Muyschondts' view that instances of considerable predation in butterflies occur when butterflies are resting or feeding, and that such predation does not come from birds. This is not meant to imply that there are instances of heavy avian predation on butterflies. Even perching aposematically-coloured and distasteful butterflies such as the Monarch, *Danaus plexippus* L. are attacked and partially eaten by certain species of birds in the wild (Calvert, Hedrick, and Brower, 99, *Science*, **204**: 847-851), and sometimes distasteful and aposematically-coloured Ithomiine butterflies in flight are plucked from the air by birds in Brazil (Brown and Neto, 1976, *Biotropica*, **8**: 146-147) and these butterflies are generally cryptic in both upper and lower wing colour patterns. Both groups of butterflies are largely confined to the lower understory forest floor, and a combination of eyespot markings and subdued wing colours or translucency, probably function to conceal these butterflies while resting and feeding. In field samples of satyrids in the genera *Antirrhoea*, *Caerois*, *Cithaerias*, *Euptlchia*, *Taygetis* and others captured or observed at rotting banana baits in Costa Rican lowland tropical rain forests over the past eight years, very few individuals had symmetrical asymmetrical wing damage, indicating a low incidence of unsuccessful attacks by insectivorous vertebrates. If these butterflies are common targets for predators the tell-tale symmetrical or asymmetrical wing damage patterns would appear more frequently in wild-caught individuals. An absence of such wing damage has been observed for *Caligo*, *Brassolis*, *Catoblepia*, *Eryphanis*, and *Opsiphanes*. The lack of flash colouration characteristic of *Morpho*, along with totally subdued colours and eyespot markings, provides effective concealment of these butterflies from insectivorous vertebrates wandering on the forest floor. Other features of these adaptations are discussed elsewhere (Young, 1979, *Journal New York Entomol. Soc.*, **87**: 66-77).

In summary, while it is probably true that most large butterflies are seldom attacked by birds when flying, those feeding or resting on or near the ground are attacked in greater frequency by other types of small insectivorous vertebrates such as teiid lizards in tropical forests. If particular species are being targets for such predators, it is expected that a certain fraction of attacks will result in near misses, resulting in butterflies having symmetrical wing damage patterns, especially along the edges of the hindwings, since presumably most of these attacks come from behind. If the predator jumps down

from a low arboreal perch, the damage may appear on the forewings. Flying butterflies attacked by birds and missed are expected to have beak-type damage to one wing. By scoring wild-caught butterflies for each type of wing damage, and excluding tattering from other sources, estimates of the frequencies of both kinds of unsuccessful attacks can be obtained. For those species of *Morpho* that fly in lower understory and have dull blue wings with large eyespots, the highest frequency of symmetrical wing damage is found; such damage, and asymmetrical damage is virtually non-existent in high-flying species with brilliant wings and small eyespots. Morphos may be best suited for upper forest understory and canopy habitats, but selection might have favoured some species occupying the lower regions of the forest, and for feeding on sweet-smelling fallen fruits and soupy fungal growth. Other groups of lower understory butterflies regularly feeding on these resources, such as the Satridae and Brassolidae, have become highly adapted to such predators since the combination of subdued colours or translucent wings and eyespots of varying size, is likely responsible for the absence of symmetrical wing damage resulting from near misses by predators. To what extent vertebrate predation on resting or feeding butterflies on the floors of tropical forests actually regulate populations of individual species remains undetermined.

THE PUPATION REQUIREMENTS OF *ECTOEDEMIA ARGENTIPEDILLA* (ZELLER). — Recently I received from Holland an interesting paper on the biology of *E. argentipedella* (Frankenhuijzen, A. van & de Vries, D., 1979. Waarnemingen aan *Ectoedemia argentipedella* (Zeller), een mineermot op berk (Lep., Nepticulidae). *Ent. Ber., Deel*, **39**: 129-135). The authors state that it is obligatory for the larvae to have soil particles with which to cover their cocoons. This is fully in accordance with my own experience and in *The Moths and Butterflies of Great Britain and Ireland*, **1**: 197, I state accordingly that the cocoon is spun on the surface of the soil.

What, then, about the 16 specimens of *E. argentipedella* I reared from a nest-box (*Entomologist's Rec. J. Var.*, **90**: 244)? I am afraid I may have made a wrong assumption and suppressed a factor which did not seem to be relevant at the time. I received the nests from the warden of Birch Wood Nature Reserve in large polythene bags, each containing more than one nest. The bag in question contained, besides tits' nests, a blackbirds' nest, doubtless from the type of nest-box with a large rectangular entrance aperture. Since the tits' nests were ideal pupation material for most nepticulids and I was forgetful of my past experience, I jumped to the conclusion that these were the source of my moths. It could have been, and probably was, the blackbirds' nest which, as almost every reader will know, is stiffened with clay. My note does not, therefore, contradict the findings of the Dutch authors on the pupation habits of this species. — A. M. EMMET, Labrey Cottage, Saffron Walden, Essex, CB11 3AF. 23.i.80.